

**BIOLOGICAL PROCESSES
IN SPACE AND TIME
CAVE LIFE IN THE LIGHT
OF MODERN EVOLUTIONARY
THEORY**

KENNETH CHRISTIANSEN

Grinnell College
Grinnell, IA 50112
U.S.A.

CONTENTS

Introduction

Modern evolutionary theory

1- Neo Darwinian paradigm

A- Core tenets

B- Extension and modification of synthesis

C- Non-conflicting theories sometimes presented as conflicting

2- Non-synthetic theories

A- Possibly but not necessarily conflicting theories

B- Real conflicting theories.

Recent evolutionary research with cave animals

Diversity of cave habitats

Genetic of cave organisms

Adaptation

Troglomorphy

Entrance, occupation and survival in caves

Evolutionary mode

Convergence, parallelism and divergence

Punctuated equilibrium

Behaviour and form

Regressive evolution

Speciation in caves and the nature of species.

The impact of Biospeleology on Evolutionary Theory

Suggested program for future research

Acknowledgements

References

ABSTRACT

That it is clear that a great deal of excellent and interesting evolutionary research has been carried on recently in biospeleology. Almost all of this work has been carried on within the limits of the Neodarwinian Paradigm and is supportive of its core tents. In spite of this there has been very little impact of this research on general evolutionary theory. This can, to some degree, be explained by failure to communicate effectively; however, to a much larger degree it can be explained by a failure to use the potential of biospeleological research to attack problems of general evolutionary interest.

Neo-Darwinian paradigm

Core tenets

1. Genetic variation is the only source of evolutionarily significant variation.
2. Selection and genetic drift are the dominant forces shaping evolution.
3. The selective process can be translated into genetic and mathematical models.
4. Fitness is defined in terms reproductive success.
5. Selection primarily involves changing gene frequencies determined by fitness.
7. Genetic drift is defined as random fixation or loss of alleles.
8. Within species evolution is a result of genetic drift+ selection with limitations set by the biological potential of the organisms involved.
9. Evolution beyond species limits are the result of processes similar to those occurring within species.
10. The direction selection takes is determined by the environment and the preexisting biological potential of the organism involved.
11. Evolutionary opportunism prevails.

Extension and modifications of synthesis

1. Wright's shifting balance model.
2. Expansion and complexing of genetic basis.
3. Evolutionary stable strategy theory.
4. Founder effect and bottleneck theories.
5. Sociobiological theory.
6. Hierarchical evolutionary theories.
7. Ecosystem evolution.
8. Group selection theories.
9. Phylogenetic constraints.
10. Simpons' adaptive shift.

Non-conflicting theories sometimes presented as conflicting

1. Punctuated equilibrium.
2. Neutral gene hypothesis.

Non-synthetic theories

Possibly but not necessarily conflicting theories

1. Gaia hypothesis.

2. Developmental constraints and moderate neo-orthogenetic theories.
3. Paradigm shift., baupläne theories.
4. Wiley & Brooks entropy theory.
5. Saunders & Ho Minimum complexity law.
6. Trans-specific gene transport theories.

Real conflicting theories

1. Species selection.
2. Evolution primarily via extinction.
3. Evolution as random walk.
4. Saltational theories.
5. Neolamarckian theories.
6. Radical neo-orthogenetic theories.

We shall examine these theories and ideas only insofar as they interface with recent biospeleology. Anyone interested in more details on the other aspects can find them in any recent evolution text.

As we review the recent work which has been done in evolutionary cave biology it should become clear that all of it is done with the acceptance and application of the core tenets of the Neo-Darwinian paradigm. Only four or the extensions of theory have been slightly dealt with: a) adaptive shift, b) founder effect, c) shifting balance and d) punctuated equilibrium. None of the conflicting theories has been applied to or analyzed in recent biospeleological works.

RECENT EVOLUTIONARY RESEARCH WITH CAVE ANIMALS

Diversity of cave habitats

Most of the early work on evolutionary cave biology was done with the idea that evolutionarily interesting cave organisms were almost all to be found in temperate zone limestone caves. Organisms living in these environments were those considered when the terms troglobite, troglophile, troglaxene were created (see Barr, 1968 for discussion of their origin) and the concept of troglomorphy developed (Christiansen, 1962). It was known that aquatic cave species were sometimes found in the groundwater or nappe phreatique, and such species were given the name *phreatobites* by Motas and Tanaschi (1946). It was also known that edaphic organisms also were sometimes found in caves. The more recent discovery of the non-calcareous Milieu Souterrain Superficiel or M.S.S. (Juberthie *et al.*, 1980) and the redefinition of marine anchialine caves (Stock & Iliffe 1986) and the identification of crevicular fauna (Hartet *al.*, 1985) have further complicated the

picture. Even more important has been the discovery of many troglomorphic forms in the lava tubes and other caves of the tropics (Howarth, 1981, 1987; Peck, 1990). These discoveries have made the previously distinct cavernicole environment fade gradually in many different directions and dimensions. One result has been the attempt to develop terms such as stygiobiont or resurrect old terms such as cryptozoic habitat (Peck, 1990) to cover all such organisms as well as others such as musicoles, lapidicoles, etc. On the other hand it is becoming increasingly clear that the inhabitants of some of these becoming increasingly clear that the inhabitants of some of these habitats respond evolutionarily quite differently from others (Danielopol & Rouch, 1991). As Barr pointed out in 1968, the semantic problem can be solved by understanding that a species may occur in caves and inhabit one or more of the cave adjuncts or vice versa; however, there are many organisms which are in fact limited to caves and very similar habitats whatever their geological origin and nature. It is these forms which so far have been shown to have the parallel and convergent evolutionary tendencies which make cave organisms so valuable for the study of evolutionary mechanisms.

Genetics of cave organisms

Any application of modern evolutionary theory to cave life requires a good understanding of the genetics of cave organisms. Fortunately the last twenty years has seen a great increase in our knowledge of this field (Sbordoni, 1980 table 4, Wilkens 1987). These studies have greatly facilitated our understanding of all evolutionary processes.

In some cases the results have, apparently, been contradictory, for example Wilkens (1988) found surface populations of *Astynax* to be highly polymorphic while the cave populations were not. Similarly Cesaroni et al. (1981) showed that troglophilic species of spiders had higher genetic variability than nearly completely troglobitic forms. In contrast Kane & Brunner (1986) found that in populations of *N. tellkampfi* genetic variability was similar to that of surface dwelling invertebrates. Some suggestion that this species may be unusual is shown by the fact that it seems to be little affected by geographic considerations (Turanchik & Kane, 1979) whereas many other species are strongly affected (Sbordoni 1980, Sbordoni et al., 1976, 1985). Peck suggests (pers. comm.) that this is a result of the great vagility of *tellkampfi* encouraging gene flow. Other cases of great differences in genetic variability exist among troglobitic species of cave carabids (Barr pers. Comm.).

Sbordoni (1980) suggests that there is a reduction in genetic variability upon entrance into caves followed by a subsequent increase. This supports Barr's (1968) model of cave colonization. Thus there should be less variability in cave than in surface populations of the same species as a result of founder effect, and

subsequent diminution due to gene drift and/or selection. There should also be increasing variability with increased troglomorphy within a specific lineage. Our own research with morphological variation in Collembola (Christiansen & Moberg, 1988) would agree with the latter but not the former. Avise and Selander's work (1972) and Cesaroni's work mentioned above on the other hand support the reduction of variability in cave as opposed to surface forms. A partial explanation of these conflicting result may be the strong correlation seen between genetic variability and environmental conditions (Delay *et al.*, 1980, Sbordoni *et al.*, 1976).

Another interesting if not surprising discovery that while interrelationships as measured by analysis of some cave independent morphological features are similar to those determined by analysis of a variety of genetic measures (Allegrucci *et al.*, 1987, Sbordoni *et al.*, 1991), cave dependant features are not. This is what would be expected if the genetic measures presently in use do not measure features of any adaptive significance to the animals.

Adaptation

Here I use this term in the sense of evolutionary modifications of the phenotype of lineages of organisms which putatively increase their chances of survival or competitiveness in caves. The topic of cave adaptation has received excellent reviews (Vandel, 1964; Barr, 1968; Culver, 1982) and I shall not repeat the evidence and discussions given there; however, Culver's conclusions are important. These are: first, that many populations are adapted to scarce food supplies, second, food scarcity is not a universally dominant selective force, third many troglophiles are not troglobites in training but truly cave adapted forms which have no gene flow with surface populations and fourth, that many cave populations are not at an evolutionary equilibrium.

Most earlier evidence to support the idea that a particular feature is an adaptation for cave life was secondary and derived from the distribution patterns in organisms having different levels of development of the features concerned. Recent works have given much better evidence from genetic analysis, ecophysiology and selective analysis which supports the idea that many of these features are in fact adaptive (Allegrucci *et al.*, 1982; Cesaroni *et al.*, 1981; Christiansen & Moberg, 1988; Culver *et al.*, 1990; Fong, 1988; Jones & Culver, 1989; Kane & Culver, 1991; Peck, 1986; Poulson, 1980; Sbordoni, 1980; Sbordoni *et al.*, 1991; Wilkens, 1987 and in this book by Culver & Kane). Almost all of these studies agree with Culver's four conclusions.

Our own studies from 1957-1960 involved large numbers of cave and surface Collembola of the family Entomobryidae. This work culminated in a paper in *Evolution* (1961) wherein we pointed out that the morphological characteristics seen in various lineages of the family could be divided into two groups. The

first group, which we called cave independent, showed no parallel or convergent evolution. The second set of characteristics, which we called cave dependent, show strong convergent and parallel evolution. The former characteristics are frequently called non-adaptive and the latter adaptive. This is probably correct for most cave independent and non-regressive cave dependant features but I feel that the terminology makes unnecessary and possibly unwarranted assumptions and prefer to use the first set of terms. It is certainly among the second set of characteristics that we can best look for adaptations and features which characterize cave animals or troglomorphy.

It is notable that while earlier works suggested non Neo-Darwinian explanations for adaptation in cave animals (see Vandel, 1964) all recent work has been done with the clear assumption of the applicability of its core tenets.

Troglomorphy

In 1962 I created the term "troglomorph" to designate those phenotypic features which were characteristic of cave animal evolution and served to identify cave adapted organisms without the unprovable and often erroneous assumption of living only in caves implied by terms such as troglobite. These are essentially the same features discussed under the rubric "Le Facies Cavernicole" (Vandel, 1964). While the term was originally used for morphological features subsequent work has shown that it applies equally well to behavioural and physiological features (Burchards *et al.*, 1985; Christiansen, 1965, 1970, 1970a; Christiansen & Culver, 1968, 1969; Hüpop, 1987; Parzefall, 1986; Peck, 1986; Sbordoni, 1980; Thibaud, 1970, 1981; Wilkens, 1988; Wilkens *et al.*, 1988). Table I summarises the major troglomorphic features.

Troglomorphy is not universal among cave organisms. The phreatobite entomostracan crustacea (Danielopol & Rouch, 1991) and the extremely edaphic collembola such as the members of the family Onychiuridae show no clear morphological troglomorphy. In many other groups the troglomorphy is questionable or inconsistent (Culver, 1982). It is also absent in cave environments such as guano piles which are extremely energy rich (Sbordoni, 1980). Stewart Peck (pers. comm.) has pointed out that troglomorphy should not be expected in these cases since it occurs only the organisms are exploiting large volume spaces such as surface of cave walls or floors (Peck, 1973) or large bodies of water. Indeed we have long noted that the troglomorphic features of cave Entomobryidae are most closely approached in two very different habitats. The foot structure is closest to that seen in aquatic Collembola but the body shape features are most similar to those seen in forms (largely tropical) which live above the litter or soil, in trees. It is interesting that something similar to troglomorphy has been found in phreatobites where small size is convergently developed via paedogenesis (Boutin & Coineau, 1990).

Table 1
Common troglomorphic characteristics

Morphological	Reference
Specialization of sensory organs (touch chemoreceptor, hygroreceptor, thermoreceptor, pressure receptor).	Sbordoni 1980
Elongation of appendages	Sbordoni 1980
Pseudophysogastry (Coleoptera)	Sbordoni, Accordi et al 1980
Reduction of eyes, pigment, wings	Sbordoni 1980
Increased egg volume	Sbordoni 1980
Unguis elongation (Collembola)	Christiansen 1961
Foot modifications (Collembola, planthoppers)	Christiansen 1961
	Howarth et al. 1990
Scale reduction or loss (Fish)	Wilkens 1988,
	Ercolini et al. 1982
Cuticle thinning (terrestrial arthropods)	Numerous
Physiological & Ethological	
Slowing metabolism	Sbordoni 1980
Relaxation & degeneration Circadian rhythms	Sbordoni 1980
Reduction or adjustment of Circannual rhythms	Sbordoni 1980
Lowered fecundity	Sbordoni 1980
Increases life span	Sbordoni 1980
Starvation resistance (Collembola)	Christiansen 1970 a,
	Thibaud 1981
Behavioural	
Locomotor patterns (Collembola)	Christiansen 1965
Decreased aggregation (Collembola)	Christiansen 1970
Reduced alarm substance reaction (Fish)	Parzefall 1986
Food seeking (Fish)	Hüpop 1987
Reduce intraspecific aggression (Fish, Collembola)	Christiansen un publ.

Where troglomorphy does occur it allows for a separate analysis of those features clearly affected by the cave environment and those which are unaffected by it. It also gives clear polarity for phylogenetic analysis and permits a measure, or least an indication of the degree of cave adaptation of different groups of organisms (Christiansen, 1961; Christiansen & Culver, 1968, 1987; Poulson, 1986).

Studies of troglomorphic evolution have produced a number of interesting ideas. There is a clear tendency for species to shift from R to K adaptation as they become increasingly cave adapted (Juberthie, 1984, 1985; Poulson, 1981; Peck, 1986; Sbordoni, 1980). Most exciting of all are the works of Culver, Kane and their collaborators on *Gammarus minus*, which unites genetic, population genetic, population dynamic and ecological analysis to answer the question as to

whether troglomorphic changes are in fact adaptive (Culver, 1987; Culver & Fong, 1986; Culver *et al.*, 1990; Culver & Kane this work; Fong, 1988; Kane & Richardson, 1990; Richardson & Kane, 1988). These works indicate that the troglomorphic features which have been studied are subject to selection and are adaptive.

Entrance, occupation, and survival in caves

The question as to how organisms entered caves in the first place and how they become adapted to cave existence has occupied a considerable amount of evolutionary investigation. All of the recent work has been done with the tacit assumption of the validity of the Neo-darwinian paradigm's core tenets. Much of the discussion and controversy on this topic has been confused by the failure to recognize that 3 very distinct levels or phenomena are involved. These are: 1) the capacity to enter and survive in caves, 2) the capacity to reproduce (surviving the genetic restriction to cave populations), spread and compete in some areas in caves, and 3) the capacity to evolve lineages of increasingly troglomorphic and competitive species within caves. Each higher numbered phenomenon presumes the lower as a precursor but each lower does not presume the higher as a result. Although probably all students of this problem recognize this distinction (Vandel, 1964; Barr, 1968; Rouch & Danielopol, 1987), the failure to codify it and treat them as different processes has resulted in the fact that the most interesting question has yet to be addressed. Why is it that there is such a huge winnowing as we pass from one level to another? What has been addressed extensively is phenomenon 1 and to a lesser extent phenomenon 2 which is often assumed as a part of 1. Phenomenon 3 has been only indirectly addressed yet it is in many ways the most interesting. Although few species pass from stage 2 to 3, the capacity for evolution given by this passage results in a greater number of species which are in stage 3 than are in stage 2. An often unexpressed but underlying concept is that it is a matter of time in the cave environment alone which determines passage from one level to another. This concept is best expressed in the idea that troglophiles are troglobites in training (Barr, 1968). While it may well be that this is so for many species, it is certainly not universal (Culver, 1982; Botosaneanu & Holsinger, 1991). This is pointed up by the fact that while members of the collembolan family Isotomidae and the subfamily Tullberginae are among the most common troglophiles world wide and among the first to occupy new cave systems, there are no troglobitic lineages of either group. Similarly there are abundant cave records of most genera of the family Sminthuridae but only the genus *Arrhopalites* has either troglophile or troglobite species.

There is general agreement that pre-adaptation (or exaptation) is crucial for entrance into caves. This exaptation may be in terms of the environment occupied by the precursors (Barr, 1968; Hart *et al.*, 1985; Hobbs *et al.*, 1977; Peck, 1972; Rouch, 1982; Rouch & Danielopol, 1987; Hoch & Howarth, 1989). Environmental

pre-adaptations of this sort are probably most important for the first of the three levels or phenomena. Some workers have discussed specific morphological or behavioural features associated with successful invasions of cave systems (Vandel, 1964; Howarth, 1987; Wilkens, 1988). Such modifications are crucial for passage to the second level. What is required for passage from level 2 to level 3 remains a mystery.

Controversy concerning entrance into and initial adaptation for cave life has been largely between those arguing for a largely relict or passive origin for cave faunas (Barr, 1968; Hobbs *et al.*, 1977; Iliffe, 1990) and those arguing for active opportunistic cave invasion (Howarth, 1987; Rouch, 1982; Rouch & Danielopol, 1987; Peck, 1990). The conflict may be much more apparent than real. Juberthie (1984) in his excellent review of the topic of cave colonization points out how the two phenomena may interlock. Botosaneanu & Holsinger (1991), while highly critical of Rouch and Danielopol's views, point out there is no essential conflict between the two concepts.

The time when extant cavernicole lineages first invaded cave systems is an interesting question. While most students have favored late Cenozoic times for terrestrial invasions (Barr, 1968; Vandel, 1964; Peck, 1984; Holsinger, 1988) aquatic forms have had accepted origins going as far back as Mesozoic (Hobbs *et al.*, 1977; Hershler & Holsinger, 1990; Manning *et al.*, 1986). These early entrance dates are necessitated by marine regression geological data. The existence of highly troglomorphic species in young aquatic caves has resulted in the postulation of former but now vanished cave systems which served as source for the extant cave faunas (Iliffe *et al.*, 1984). Part of the impetus for the idea of late Cenozoic entry of terrestrial species was the idea that the extinction of surface ancestors was essential for speciation in caves (Peck, 1984; Barr, 1968) but recent research has given evidence that many times when there are surface populations of a species present there is very little or no gene exchange between these and the populations adapted to caves (Barr, 1968; Christiansen & Culver, 1969; Wilkens & Hüpop, 1986; Wilkens, 1988; Mitchell *et al.*, 1977; Kane & Culver, 1991; and Culver & Kane this work). These facts suggest that we should re-examine the background assumptions about the times of initial cave colonization.

Evolutionary mode

Convergence, parallelism and divergence.

There is general agreement that parallelism and convergence are common in the evolution of cave animals (Barr, 1968; Culver, 1982; Culver & Fong, 1986; Vandel, 1964) but little detailed research on the topic has been carried out except

for the case of regressive features. Hüpop (1987) among others discussed the question of convergent compensatory sensory expansion and Wilkens looked at a variety of convergent and parallel developments in cave fish. We have worked with this topic in Collembola (Christiansen, 1961; Christiansen & Culver, 1968) but other works which deal with the topic do so only marginally. There are many indications that it must have occurred as is shown by evidences of multiple invasions of a single phenospecies (Barr, 1968, 1985; Culver, 1982; Culver *et al.*, 1990; Kane & Culver, 1991; Culver & Kane, in this work; Mitchell *et al.*, 1977; Hobbs *et al.*, 1977), and strong evidence of little correlation between genetic and morphological similarity of cave forms (Sbordoni *et al.*, 1987).

Divergence has received considerably more attention. Since most of this work concerns the process of speciation I shall deal with in more detail in that section.

Punctuated equilibrium

One topic of considerable interest has been the question of the role of punctuated equilibrium in the evolution of cave life. Discussion of this topic is complicated by the various versions of the hypothesis which have been present (Gayon, 1990); however, the strong version (Gould & Eldredge, 1986) is that adaptive change is limited to the time during which the process of speciation occurs. This is not supported by present studies of cave organisms (Culver, 1987; Christiansen & Moberg, 1988; Howarth, 1987). These studies rather support a view that while more change occurs during speciation than otherwise but that significant change does occur within the limits of a single species.

Behaviour and form

More and more studies of the behaviour of cave animals are being done; however, relatively little has been done to show the evolutionary link between changes in behaviour and changes in form. Our works on Collembola (Christiansen, 1965; Christiansen & Culver, 1968), Poulson's work on Amblyopsid fish (1963) and Wilkens (1988), Hüpop (1987) and their co-workers are the only ones I am aware of. This is a fertile field for future study. It is almost certain that the kind of interaction shown in the above mentioned works is widespread in cave animals.

Regressive evolution

This is the evolutionary mode which has been best studied by far in cave organisms. This is hardly surprising since cave animals have used to bolster one or another evolutionary theory from the start (Kane & Richardson, 1985; Richardson & Kane, 1988). Recent works have extended the range of regressive features from the well known morphological to behaviour (Burchards

et al., 1985; Parzefall, 1986; Poulson & Jegla, 1969; Lamprecht & Weber, 1982, 1986; Martin & Weber, 1985; Weber, 1986). Drawing on Barr's 1968 work we earlier (Christiansen, 1985) listed 14 theories which had been used to explain regressive evolution. As Sbordoni (1980) pointed out some of these are of merely historical interest. I would consider Lamarckism (neo o paleo) Orthogenesis, and Vandel's organicism to be such theories. Recent works reaffirm the validity of the core tenets of the Neo-Darwinian paradigm. Fong & Culver's work (1985) would seem to deal a death blow to both Lankester's escape theory and Ludwig's trap theory. Most of the recent works have been in support of either a view that regression involves some form of genetic degeneration due to mutation accumulation (Poulson, 1985; Howarth, 1987; Wilkens, 1979, 1982, 1988, and this work; Wilkens *et al.*, 1988) or some form of positive selection associated with reduction (Sket, 1985; Kane & Richardson, 199; Culver *et al.*, 1990; Culver & Kane, this work). Recently studies with carabid beetles have suggested that the reduced eyes of some moderately troglomorphic beetles are under normalizing suggestion (Bartkowiak *et al.*, 1991). This would suggest that it is possible for eyes to regress while they still are of adaptive value to the animals. Examination of a number of hypotheses such as Regal's noise suppression hypothesis (1977) have not been carried out with cave animals, and others such as negative allometry only marginally investigated (Sbordoni & Sbordoni, 1973; Sbordoni *et al.*, 1976). Wilkens's work (Wilkens *et al.*, 1979; Wilkens, 1988; Wilkens *et al.*, 1988) is remarkably good at laying out the case for regressive evolution as a result of degenerative gene accumulation. On the other hand Kane and Culver's various works are very effective in demonstrating that in the case of *Gammarus minus*, selection best explains the reductive evolution. Our own work (Christiansen, 1985) which involved regressive evolution in both cave and soil forms, seems to negate the possibility that any one theory can explain all cases, even when the characters involved have clearly lost all function. Any theory which applied to all cases we studied would have to be able to produce: a) positive, negative or no correlation between features undergoing regressive evolution in the same conditions, and b) differ strikingly in different habitats, and c) allow for great variation in results while showing overall parallel evolutionary features. It is difficult to see how any extant theory can fit all these criteria. In particular the accumulation of random neutral variations can hardly produce positive and negative correlations between the same characteristics in different groups. It is also hard to see how accumulation of mutations could fail to show correlation between the regression of clearly functionless features such as eyes and furcula in soil forms. It seems much more likely that regressive evolution is produced by a variety of mechanisms with mechanism determined by the habitat and the animal group involved. We are far from having resolved what is the array of mechanisms which can be operating in cave animal evolution.

Speciation in caves and the nature of species

Speciation in cave animals has been effectively reviewed by Barr & Holsinger (1985). Further examination of speciation in aquatic cavernicoles is given in this work by Coineau & Boutin. Readers are referred to these works for extensive analysis of the general models and data used by researchers in the field. Since the Barr & Holsinger review some workers have emphasized the suitability of the Wrightian adaptive shift model (Howarth, 1987; Culver, 1987). While earlier works generally supported a strictly allopatric model for cave animal speciation (Barr, 1968; Sbordonì, 1982; Vandel, 1964) recently investigators have offered new evidence supporting parapatric (Howarth, 1987; Peck, 1990) or peripatric (Sbordonì *et al.*, 1985) speciation. All clearly operate within the limits of the Neo-Darwinian paradigm.

A difficulty with all discussions of speciation is the fact that there is an underlying assumption that what is being discussed are species which conform to the biological species model. This model assumes that genetic isolation is the key factor associated with species formation and that gene exchange is the cement which holds a species together. In some cases, where a given bisexual species is generally confined to a region where underground movement between cave habitats is possible this model may apply. This appears to be true for beetles in many cases (Peck, 1984; Barr, 1985 & pers. comm.). In many cases the model is either questionable or clearly inapplicable. In the first place we have the fact that gene flow is not essential to maintaining species identity as is shown by the existence of species in asexual organisms, (Holman, 1987; Shapeshnikov, 1984) which are quite comparable to those seen in sexual species. Similarly in the collembola a number of cave groups have both parthenogenetic and bisexual forms and the nature of the phenotypic species is indistinguishable between them. A second problem is faced by the assumption that spatially separated cave systems with geological or river barriers to gene flow, which harbor the same species of cave organisms are kept as one species by occasional interchange via surface populations. The evidence is very strong that even when large surface populations of the same species exist there is rarely significant gene interchange between these (Caccone & Sbordonì, 1987; Kane & Culver, 1991; Culver & Kane, this work; Wilkens, 1988; Wilkens *et al.*, 1988; Christiansen & Culver, 1969). Furthermore since the biological species concept depends on gene flow and cave species with very few exceptions are determined on phenotype the model requires similarity or pattern between the two. The evidence so far available rarely supports this idea (Allegrucci *et al.*, 1992; Hüpop, 1987; Caccone & Sbordonì, 1987; Wilkens, 1988; Sbordonì *et al.*, 1985, 1987, 1988).

In view of the improbability that the biological species model is generally applicable to cave organisms its general use can only be explained by fad and convenience. Its clarity of definition probably results in its general use; however,

this may be a case of "searching for the keys, which we lost in the yard, under the street-lamp because the light is better there".

What model or models should we use? No area in biology is so fraught with controversy (Gayon, 1990). By my last count there were at least 15 distinguishable definitions proposed by students of the question. If we accept Ghiselin's concept (1974) that species are individuals then we have to consider each case as *sui generis*. Our early work (Christiansen & Culver, 1968) led us to the little noted nor long remembered concept of parallel speciation. The only species concept which fits with this idea is the evolutionary one such as "a species as a single lineage of ancestral decedent populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1978) or "an internally similar part of a phylogenetic tree" (Willis, 1981). It is important that before we analyze speciation in any group we answer the question: what model of the species best fits the data in this group? It may well be, as appears likely for most cave beetles, that the biological species model best fits the data; however, this should only be accepted after the other models have been tested against the data to see if they fit them better.

THE IMPACT OF BIOSPELEOLOGY ON EVOLUTIONARY THEORY

This brief overview shows that there has been a great deal of biospeleological research dealing with the mechanism and results of evolution. In spite of this there has been almost no evidence of this work in recent general papers or books dealing with the large problems or major controversies concerning evolutionary theory. If we look at recent philosophical analyses of the controversies about the modern synthesis (Naylor & Hanford, 1985; Burian, 1988; Gayon, 1990; Grene, 1990) or attempts at revision or clarification of the modern synthesis (Ho & Saunders, 1984; Dawkins, 1986; Endler & McLellan, 1988), there is almost never any reference to biospeleological work even when examples from the field are appropriate and readily available, as in the case of pre-adaptation.

Why this lack of impact? It can in part be explained by a lack of communication. Few biospeleological studies of great general interest are published in journals such *Biotheoretica*, *Evolution*, *American Naturalist*, or *Evolutionary Theory*, which are generally read by other students of evolution, who are not interested in cave animals.

A second, (and probably more important) reason for the lack of impact is the fact that we have not addressed many of the major controversies which excite the evolutionary theorists. If you examine the evolutionary theories shown earlier which have generated major controversies it is clear that only one- regressive evolution- has been extensively dealt with by biospeleologists. Adaptation and

punctuated equilibrium have been given a little attention but we have hardly touched any of the others. It is true some topics such as sociobiology are not applicable to cave organisms but many which we now totally ignore are suitable topics for investigation. Until we start to address these I fear that our work will continue to be ignored by the bulk of evolutionary theorists, who view caves as curiosities and not what they are, an ideal arena for the study of most evolutionary processes.

SUGGESTED PROGRAM FOR FUTURE RESEARCH

Unless we wish to remain a group of workers talking almost exclusively to each other, I think it is clear that we must do some things differently. First I think we must try to communicate better with people outside the field. This can be done, as suggested earlier by writing papers appropriate for general theoretical journals. It can also be addressed by trying to get into symposia or meetings dealing with general evolutionary mechanisms and demonstrating appropriateness of biospeleological studies.

Before we can do this extensively our studies must be of a sort that can generate widespread interest. Caves, as we all know, are natural evolutionary laboratories. Their peculiar conditions afford an opportunity to study evolution under much more comprehensible conditions than generally obtain. We need to take much greater advantage of this fact. As I see there are 7 controversial areas of study where caves should furnish a unique opportunity for effective analysis.

First, we should certainly continue to deal with the question of regressive evolution. This is one area where, I believe, we have invested a sufficient amount (if not too much) of our resources and time.

Second, I feel that we have a good start on the relative roles of gradualism and punctuation in evolution and should continue to work on this problem. The isolation of different cave populations, the persistence of populations showing different levels of adaptation as measured by degrees of troglomorphy, and our increasing knowledge of the genetics of cave animals all makes these ideal subjects for testing the hypothesis that significant adaptation takes place only during the process of speciation.

Third, we have also made a good start at understanding the process of adaptation as it obtains in cave animals; however, I fear that the problems of this study may be one of the most difficult to resolve. In groups where clear troglomorphy occurs we do have good indicators at the kinds of organs and behaviours which should be studied to analyze adaptation. We need many more studies such as those of Culver and Kane demonstrating the fitness values of characteristics, and those of Wilkens, Hüppop, Sbordoni and their collaborators and our own laboratory, demonstrating the adaptive nature of different troglomorphic features. The difficulty

lies in the great time and resource requirement of such studies. We most desperately need someone to carefully review the presently available research to see what evidence we have and what we need to determine the importance and role of adaptation in the evolutionary process seen in cave animals. Until that is done we will have only a poor view of exactly what are the most important questions to ask.

Fourth, no biospeleologist has to my knowledge addressed the question of species selection. Most extant hierarchical schemes require that species selection be a real and important process. Caves with their unique assembly of primitive and advanced species of the same lineage should be ideal for establishing the existence or absence of this process. Somebody should be able to figure out what patterns of geographic distribution and replacement would obtain if species selection were a significant evolutionary mode, and what pattern would obtain if it were not. Then the distributions of various groups could be matched to the models to see which had the better fit.

Fifth, we need to turn to the question of the relative importance of random as opposed to deterministic selective factors in shaping the course of evolution. A concept championed by S.J. Gould and others is that evolution is not predictive, that is largely the result of random factors. To use Gould's phraseology "If we played the tape of evolution back every replay would produce a strikingly different outcome" (Gould, 1989). Caves furnish us historical situations where the tape has already been "experimentally" replayed many hundreds of times and in many cases given us a pretty good recording in the form of extant forms of cave life. Somebody should look over all the data and see just how valid the concept is applied to cave life.

Sixth the question of whether or not natural selection can accomplish macroevolutionary change could be addressed. The fact that caves often have species or even populations of one species at strikingly different levels of troglomorphy furnishes an opportunity to deal with this question very effectively. If a series of populations of a slightly troglomorphic species or populations showing different levels of troglomorphy could be studied using modern genetic analytical techniques the nature of the changes associated with the increasing troglomorphy could be determined. The same thing could then be done between species showing the greatest troglomorphy. If natural selection, proceeding in the accepted Neodarwinian mode is the mechanism bringing all these changes about then the genetic differences between the slightly troglomorphic groups and those between the slightly and highly troglomorphic forms should be similar but qualitatively the same or there are differences between the forms showing very great troglomorphy and slight troglomorphy which are qualitatively different from those seen between slightly troglomorphic forms, then a different mechanism may be indicated. It may well be that the data for resolving this is already available in some of the works discussed earlier and merely needs reworking.

Seventh I think that cave animals should furnish an excellent tool for helping resolve the question of the nature of species. It is very probable that extant data is adequate for someone to analyze it with a mind to seeing which of the many species concepts presently floating about best fits the situation in different groups. As mentioned earlier, it seems very unlikely that one model will be able to fit all groups but how many different ones are required? It could well be that cave like is an almost definitive set of organisms to support or deny the concept of species as individuals. On the other hand it is also possible that some new data sets are required to do this. We will only know when somebody tackles the problem on a broad scale.

In addition to these controversial areas of study there are a number of non-controversial fields which also offer unexplored but potentially very generally rewarding studies. Two which immediately come to mind are the nature of E.S.S. mechanisms and the role of phylogenetic constraints in determining evolution. The repetitive and limiting nature of the cave environment should furnish ideal situations to analyze these phenomena.

If these controversies and questions were dealt with there is in my mind no doubt that cave research would have a far greater impact on the study of evolution than it historically has had.

ACKNOWLEDGEMENTS

This research was supported by grants from Grinnell College. The author would like to thank Thomas Barr, David Culver, and Pere Alberch for their helpful comments and suggestions. Particular thanks are due to Stewart Peck whose detailed and thoughtful analysis was most helpful.

REFERENCES CITED

- ACCORDI, F., M. RAMPINI & V. SBORDONI, 1980. Ultrastructure of the cuticle of false physogastry in Cavernicolous Bathyscini. *Acts XII Nat. Congr. Ent.*, 2: 79-86.
- ALLEGRUCCI, G.A., C. CACCONE, D. CESARONI, M. SBORDONI, E. MATTAEIS de & V. Sbordonì, 1982. Natural and experimental interspecific hybridization between populations of *Dolichopoda* cave crickets. *Experientia*, 38: 96-98.
- ALLEGRUCCI, G.A., F. BALDARI, D. CAESARONI, R.S. THORPE, & V. SBORDONI, 1992. Morphometric analysis of interspecific variation of crayfish from a Mexican cave. *Biol. J. Linn. Soc.* (in press).
- ALLEGRUCCI, G.D., D. CESARONI & V. SBORDONI, 1987. Adaptation and speciation of *Dolichopoda* cave crickets (Orthoptera, Rhaphidophoridae): geographic variation of morphometric indices and allozyme frequencies. *Biol. J. Linn. Soc.*, 31: 151-160.

- AVISE, J.C. & R.K. SELANDER. 1972. Genetics of cave dwelling fishes of the genus *Astynax*. *Evol.*, 26: 1-19.
- BARR, T.C.. 1968. Cave ecology and the evolution of troglobites. *Evolutionary Biology*, 2: 35-102.
- BARR, T.. 1985. *Pattern and process in speciation of trechine beetles in eastern North America (Coleoptera: Carabidae: Trechinae)*. Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. G.E. Ball (ed.): 350-407.
- BARR, T.C., Jr. & J.R. HOLSINGER. 1985. Speciation in cave faunas. *Ann. Rev. Ecol. Syst.*, 16: 313-337.
- BARTKOWIAK, D.; T. TSCHARNTKE & F. WEBER. 1991. The effects of stabilizing selection on the regressive evolution of compound eyes in hypogean carabid beetles. *Mem. Biospeol.*, 16: 19-24.
- BOTOSANEAL, L. & J.R. HOLSINGER. 1991. Some aspects concerning colonization of the subterranean realm- especially of subterranean waters: a response to Rouch & Danielopol. 1987*. *Stygologia*, 6(1): 11-39.
- BOUTIN, C. & N. COINEAU. 1990. "Regression model" "model biphasé" d'évolution et d'origine des micro-organismes stygobies interstitiels continentaux. *Rev. de Micropaléontologie*, 33: 303-322.
- BURCHARDS, H.; A. DOLLO and J. PARZEFALL. 1985. Aggressive behaviour of an epigeal population of *Astynax mexicanus* and some observations on 3 subterranean populations. *Behav. Processes*, 11(3): 225-236.
- BURIAN, R.. 1988. Challenges to the evolutionary synthesis. *Evolutionary Biology*, 23: 247-269.
- CACCONE, M. & V. SBORDONI. 1987. Molecular evolutionary divergence among North American cave crickets. I. Allozyme variation. *Evol.*, 41(6): 1198-1214.
- CESARONI, D.; G. ALLEGRI; A. CACCONE; M. COBOLLI-SBORDONI; E. de MATTHAEIS; M. Di RAO & V. SBORDONI. 1981. Genetic variability and divergence between populations and species of *Nesticus* cave spiders. *Genetica*, 56: 81-92.
- CHRISTIANSEN, K.. 1961. Convergence and parallelism in cave Entomobryinae. *Evol.*, 15(3): 288-301.
- CHRISTIANSEN, K.. 1962. Proposition pour la classification des animaux cavernicoles. *Speleol.*, 2: 76-78.
- CHRISTIANSEN, K.. 1965. Behaviour and form in the evolution of cave Collembola. *Evol.*, 19(4): 529-532.
- CHRISTIANSEN, K.. 1970. Experimental studies in aggregation and dispersion of Collembola. *Pedobiologia*, 10: 180-190.
- CHRISTIANSEN, K. , 1970a. Survival of Collembola on clay substrates with and without food added. *Annales de Speleol.*, 25(46): 849-852.
- CHRISTIANSEN, K.. 1985. Regressive evolution in Collembola. *N.S.S. Bull.*, 47(2): 89-100.

- CHRISTIANSEN, K. & D. CULVER, 1968. Geographical variation and evolution in *Pseudosinella hirsuta*. *Evolution*, 22(2): 237-255.
- CHRISTIANSEN, K. & D. CULVER, 1969. Geographic variation and evolution in *Pseudosinella violenta*. *Evolution*, 23(4): 602-621.
- CHRISTIANSEN, K. & D. CULVER, 1987. Biogeography and distribution of cave Collembola. *J. Biogeography*, 14: 459-477.
- CHRISTIANSEN, K. & T. MOBERG, 1988. *Pseudosinella* revisited. *Int. J. Speleol.*, 17: 1-20.
- CULVER, D.C., 1982. *Cave Life*. Harvard Univ. Press. 189 pp.
- CULVER, D.C., 1987. The role of gradualism and punctuation in cave adaptation. *Int. J. Speleol.*, 16: 17-31.
- CULVER, D.C. & D.W. FONG, 1986. Why all cave animals look alike. *Stygologia*, 2(3): 208-216.
- CULVER, D.C.; T.C. KANE; D.W. FONG; R. JONES; M.A. TAYLOR & S.C. SAUERISEN, 1990. Morphology of cave organisms- is it adaptive?. *Mem. Biospeol.*, 17: 13-26.
- DANIELOPOL, D.L. & R. ROUCH, 1991. L'adaptation des organismes au milieu aquatique souterrain. Réflexions sur l'apport de recherches écologiques récentes. *Stygologia*, 6(3): 129-142.
- DAWKINS, R., 1986. *The Blind watchmaker*. Penguin Books: 1-318.
- DELAY, B.; V. SBORDONI; M. COBOLLI-SBORDONI & E. MATTHAEIS, 1980. Divergences genetiques entre les populations de *Speonomus delarouzei* du Massif de Canigou. *Mem. Biospeol.*, 7: 235-247.
- ENDLER, J.A. & T. McLELLAN, 1988. The processes of evolution: toward a newer synthesis. *Ann. Rev. Ecol. Syst.*, 19: 395-421.
- ERCOLINI, A.R.; BERTI, L. CHELAZZI & G. MESSANA, 1982. Researches on the phreatobitic fishes of Somalia: Achievements and prospects. *Monitore Zool. Italiano, Suppl.*, 17(9): 219-241.
- FONG, D.W., 1988. Morphological evolution of the amphipod *Gammarus minus* in caves: quantitative genetic analysis. *Am. Midl. Nat.*, 121: 361-378.
- FONG, D.W. & D. CULVER, 1985. A reconsideration of Ludwig's differential migration theory of regressive evolution. *N.S.S. Bull.*, 47(2): 123-127.
- GAYON, J., 1990. Critics and criticisms of the modern synthesis. *Evolutionary Biology*, 24: 1-50.
- GHISELIN, S.J., 1974. A radical solution to the species problem. *Syst. Zool.*, 23: 536-544.
- GOULD, S.J., 1989. *Wonderful life: The Burgess shale and the nature of history*. Norton: 1-347.
- GOULD, S.J. & N. ELDREDGE, 1986. Punctuated equilibrium at the 3rd stage. *Syst. Zool.*, 35: 143-148.
- GRENE, M., 1990. Is evolution at a crossroads?. *Evolutionary Biology*, 24: 51-81.

- HART, C.W. JR.; R.B. MANNING & T.M. ILIFFE, 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proc. Biol. Soc. Wash.*, 98(1): 288-292.
- HERSHLER, R. & J. HOLSINGER, 1990. Zoogeography of North American hydrobiid cavesnails. *Stygologia*, 5(1): 1-16.
- HO, M-W. & D. SAUNDERS, (eds.), 1984. *Beyond Neo-Darwinism*. Academic Press: 1-362.
- HOBBS, H.; H.H. HOBBS & M.A. DANIEL, 1977. A review of the troglobitic decapod crustaceans of the Americas. *Smithsonian Contrib. Zool.*, 244: 1-183.
- HOCH, H. & F.G. HOWARTH, 1989. The evolution of cave-adapted cixiid planthoppers in volcanic and limestone caves in North Queensland, Australia (Homoptera: Fulgoroidea). *Mem. Biospeol.*, 16: 17-24.
- HOLMAN, E. 1987. Recognizability of sexual and asexual species in rotifers. *Syst. Zool.*, 36(4): 381-386.
- HOLSINGER, J., 1988. Troglobites: the evolution of cave-dwelling organisms. *American Scientist*, 76: 147-153.
- HOWARTH, F.G., 1981. Non-relictual terrestrial troglobites in tropical Hawaiian caves. *Proc. VIII Int. Congress Speleology*: 539-541.
- HOWARTH, F.G., 1987. The evolution of non-relictual tropical troglobites. *Int. J. Speleol.*, 16: 1-16.
- HÜPPOP, K., 1987. Food-finding ability in cave fish (*Astynax fasciatus*). *Int. J. Speleol.*, 16: 59-66.
- ILIFFE, T., 1990. Crevicular dispersal of marine cave faunas. *Mem. Biospeol.*, 17: 93-96.
- ILIFFE, T.; H. WILKENS; J. PARZEFALL & D. WILLIAMS, 1984. Marine lava cave fauna: composition, biogeography and origins. *Science*, 225: 309-311.
- JONES, R. & D. CULVER., 1989. Evidence for selection on sensory structures in a cave population of *Gammarus minus* (Amphipoda). *Evol.*, 43(3): 688-693.
- JUBERTHIE, C., 1984. La colonisation du milieu souterrain; theories et modeles relation avec la speciation et l'evolution souterraine. *Mem. Biospeol.*, 11: 65-102.
- JUBERTHIE, C., 1985. Cycle vital de *Telema tenella* dans la grotte-laboratoire de Moulis et strategies de reproduction chez les araignees cavernicoles. *Mem. Biospeol.*, 12: 77-89.
- JUBERTHIE, C.; B. DELAY & M. BOUILLON, 1980. Sur l'existence d'un milieu souterrain superficiel en zone non calcaire. *C.R. Acad. Sc. Paris*, 290: 49-52.
- KANE, T. & R. RICHARDSON, 1991. The evolution of troglobites *Gammarus minus* (Amphipoda: Gammaridae) as a case study. *Mem. Biospeol.*, 18: 3-14.
- KANE, T. & R. RICHARDSON, 1990. The phenotype as the level of selection: cave organisms as model systems. *P.S.A.*, 1: 151-164.
- KANE, T. & G. BRUNNER, 1986. Geographic variation in the cave beetle *Neaphaenops tellkampfi* (Coleoptera: Carabidae). *Psyche*, 93(3-4): 231-250.

- LAMPRECHT, G. & F. WEBER, 1982. A test for the biological significance of circadian clocks: evolutionary regression of the time measuring ability in cavernicolous animals. In: Environmental Adaptation and Evolution, D. Mossakowski and G. Roth, eds., Gustav Fischer, Stuttgart/New York: 151-178.
- LAMPRECHT, G. & F. WEBER, 1986. Time-keeping mechanisms and their ecological significance in cavernicolous animals. *N.S.S. Bull.*, 47(2): 147-162.
- MANNING, R.: C.W.Jr. HART & T.M. ILIFFE, 1986. Mesozoic relicts in marine caves of Bermuda. *Stygologia*, 2(1): 156-166.
- MARTIN, W. & F. WEBER, 1985. Regression of the time-keeping ability in carabid beetles by phylogenetic adaptation to cave conditions. *Z. Naturforsch.*, 40: 438-445.
- MITCHELL, R.W.: W.H. RUSSELL & W.R. ELLIOTT, 1977. Mexican eyeless carachin fishes, genus *Astynax* environment, distribution and evolution. *Special publications, the Museum, Texas Tech. Univ.*, 12: 1-89.
- MOTAS, C. & J. TANASCHI, 1946. Acaries phreaticoles de Transylvanie. *Notat. Biol. (Bucharest)*, 4: 56-78.
- NAYLOR, B. & P. HANDFORD, 1985. In defense of Darwin's theory. *Bioscience*, 35(8): 478-484.
- PARZEFALL, J., 1986. On the heredity of behaviour patterns in cave animals and their epigeal relatives. *N.S.S. Bull.*, 47: 128-135.
- PECK, S.B., 1984. The distribution and evolution of cavernicolous *Ptomophagus* beetles in the southeastern U.S. (Coleoptera: Leiodidae: Cholevinae) with new species and records. *Canadian J. of Zoology*, 62(4): 730-740.
- PECK, S.B., 1986. Evolution of adult morphology and life-history characters in cavernicolous *Ptomophagus* beetles. *Evol.*, 40(5): 1021-1030.
- PECK, S.B., 1990. Eyesless arthropods of the Galapagos Islands, Ecuador: composition and origin of the Cryptozoic fauna of a young, tropical oceanic archipelago. *Biotropica*, 22(4): 366-381.
- POULSON, T., 1963. Cave adaptation in Amblyopsid fishes. *Amer. mid. Nat.*, 70: 257-290.
- POULSON T.L., 1981. Variation in life history of Linyphiid cave spiders. *Proc. VIII Int. Congress Speleology*: 60-62.
- POULSON, T.L., 1985. Evolutionary reduction by neutral mutations. *N.S.S. Bull.*, 47(2): 109-117.
- POULSON, T.L., 1986. Evolutionary reduction by neutral mutations: Plausibility arguments and data from amblyopsid fishes and linyphiid spiders. *N.S.S. Bull.*, 47 (2): 109-117.
- POULSON, T.L. & T. JEGLA, 1969. Circadian rythms in cave animals. *Proc. IV Int. Congress Speleology*, Luljiana Yugoslavia, 4-5: 193-195.
- REGAL, P., 1977. Evolutionary loss of useless features: is it noise suppression? *Amer. Nat.*, 111: 123-133.
- RICHARDSON, R. & T. KANE, 1988. *Orthogenesis and evolution in the 19th century: ...* In *Evolutionary Progress*, I. Nitecki ed.: 149-167.

- ROUCH, R., 1982. La systeme Karstique du Baget XII. *Annls. Limnologique*, 18(1): 41-54.
- ROUCH, R. & D. DANIELOPOL, 1987. L'origine de la faune aquatique souterraine, entre le paradigme du refuge et le modele de la colonisation active. *Stygologia*, 3(4): 345-372.
- SBORDONI, V., 1980. Strategie adattative negli animali cavernicoli: uno studio di genetica ed ecologia di popolazione. *Proc. Acad. National de Lincei*, no. 51: 61-100.
- SBORDONI, V., 1982. In Advances in speciation of cave animals. Mechanisms of Speciation. *A.R. Liss, Inc.*, N.Y. 219-240.
- SBORDONI, V. & M. COBULLI-SBORDONI, 1973. Aspetti ecologici ed evolutioniri del poplamento di grotte temperate e tropicali: Osservazioni sul ciclu biologico di alcune species de *Ptomaphagus*. *Int. J. Speleol.*, 5: 337-347.
- SBORDONI, V.; M. SBORDONI & E. de MATTAHEIS, 1976. Divergenza genetica tra popolazioni e specie ipogee ed epigee di *Niphargus* (Crustacea, Amphipoda). *Estratto da Lavori della Soc. Ital. di Biogeografia*, nuova serie, 4: 1-23.
- SBORDONI, V.; G. ALLEGRUCCI; F. BALDARI & D. CESARONI, 1988. Evolutionary genetics and morphometrics of a cave crayfish population from Chiapas (Mexico). *Int. J. Speleol.*, 17(1-4): 65-80.
- SBORDONI, V.; G. ALLEGRUCCI; A. CACCONE; G. CARCHINI & D. CESARONI, 1987. *Microevolutionary studies in Dolichopodinae cave crickets*. Bacetti: Evolutionary Biology of Orthopteroid Insects. chap. 47: 514-540.
- SBORDONI, V.; G. ALLEGRUCCI; D. CESARONI; M. SBORDONI & E. de MATTHAEIS, 1985. Genetic structure of populations and species of Dolichopods cave crickets: evidence of peripatric divergence. *Boll. Zool.*, 52: 139-156.
- SBORDONI, V.; G. ALLEGRUCCI & D. CESARONI, 1991. *A multidimensional approach to the evolution and systematics of Dolichopoda cave crickets*. NATO ASI Series, vol. H57. Molecular Techniques in Taxonomy. Springer-Verlag, Berlin: 171-199.
- SHAPESHNIKOV, G., 1984. Aphids and a step towards the universal species concept. *Evolutionary Theory*, 7(1): 1-40.
- SKET, B., 1985. Why all cave animals do not look alike: a discussion of the adaptive value of reduction processes. *N.S.S. Bull.*, 47(2): 78-85.
- SKET, J.H. & T. ILIFFE, 1986. The Concept of "anchialine" reconsidered. *Stygologia*, 2.
- THIBAUD, J.-M., 1970. Biologie et ecologie des Collemboles Hypogastruridae edaphiques et cavernicoles. *Mem. Museum National D'hist. Nat.*, 61(3): 86-197.
- THIBAUD, J.-M., 1981. Limite temporelle de resistance au jeune partiel chez les insectes Collemboles cavernicoles. *Rev. Biol. Ecol. Sol.*, 18(3): 391-396.
- TURANCHIK, E. & T. KANE, 1979. Ecological genetics of the cave beetle *Neaphanops tellkampfi* (Coleoptera: Carabidae). *Oecologia* (Berl.), 44: 63-67.

- VANDEL, A., 1964. *Biospeleologie- la biologie des animaux cavernicoles*. Gauthier-Villars (ed.), Paris. 619 pp.
- WEBER, F., 1986. Stochastic control of locomotion in carabid beetles. *5th Mtg. European Carabidologists at Stara Brda Piska*, Poland: 59-78.
- WILEY, E.O., 1978. The evolutionary species concept reconsidered. *Syst. Zool.*, 27: 17-26.
- WILKENS, H., 1979. Principles of regressive Evolution. *Verh. Dtsch. Zool. Ges.* 1979: 123-140.
- WILKENS, H., 1982. Regressive evolution and phylogenetic age: the history of colonization of fresh waters of Yucatan by fish and crustacea. *Assoc. Mexican Cave Stud. Bull.*, 8: 237-243. *Texas Mem. Bull.*, 28 (1982): 237-243.
- WILKENS, H., 1987. Genetic analysis of evolutionary process. *Int. J. Speleol.*, 16: 33-58.
- WILKENS, H., 1988. Evolution and genetics of epigeal and cave *Astynax fasciatus* (Characidae, Pisces): support for the neutral mutation theory. *Evolutionary Biology*, 23: 271-367.
- WILKENS, H. & K. HÜPPOP, 1986. Sympatric speciation in cave fishes? *Zeits. f. zool. Systematik u. Evolutionsforschung*, 24(3): 223-230.
- WILKENS, H.; N. PETERS & C. SCHEMMEL, 1979. Principles of regressive evolution. *Verh. Dtsch. Zool. Ges.*: 123-140.
- WILKENS, H.; U. STRECKER, & J. YAGER, 1988. Eye reduction and phylogenetic age in ophidiiform cave fish. *Z. zool. Syst. Evolut.-forsch.*, 27: 126-134.
- WILLIS, E.O., 1981. Is the species an interbreeding unit or an internally similar part of a phylogenetic tree?. *Syst. Zool.*, 30: 84-85.